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Tastes of Fifteen Halide Salts Following Water and NaCl: Anion and Cation Effects

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MURPHY, C., A. V. CARDELLO AND J. G. BRAND. *Tastes of fifteen halide salts following water and NaCl: Anion and cation effects.* PHYSIOL. BEHAV. 26(6) 1083–1095, 1981.—The present study investigated the tastes of 15 halide salts (LiCl, LiBr, LiI, NaCl, NaBr, NaI, KCl, KBr, KI, RbCl, RbBr, RbI, CsCl, CsBr, CsI) as a function of concentration. Taste quality and intensity judgments were made by 10 subjects following both a distilled water rinse and a 0.5 M sodium chloride rinse. For each of the 15 salts, taste quality differences were observed as a function of concentration. In addition, the non-salty tastes of the compounds exhibited complex mixture interactions with each other and with perceived saltiness. Cross-adaptation by NaCl released the mixture suppression produced by saltiness. Both cation and anion contributed to the taste of halide salts. Heavier cations and anions produced more bitter-tasting salts. While the weight of the cation had no consistent effect on perceived saltiness, lighter anions produced saltier-tasting salts.

Taste quality   Halide salts   Mixture interactions   Mixture suppression   Cross-adaptation
Magnitude estimation

IT has been demonstrated that the taste qualities elicited by the common halide salts (e.g., NaCl, KCl, LiCl) are concentration dependent [12, 13, 18, 20, 30]. These salts typically taste sweet at low concentrations, sour and/or bitter at mid-range and salty at higher concentrations. The concentration dependency of the taste qualities of the less common halides has yet to be systematically investigated. As a result, the opportunity to examine the relative effects of anion and cation on the magnitude of the taste qualities of this class of salts has been restricted. Although several previous investigators [15, 18, 19, 30] have attempted to assess psychophysically the independent roles of cation and anion on the taste of salts, few were able to examine more than a small number of salts, not all recorded quality responses other than salty, and none employed the psychophysical method of magnitude estimation. Resultant inconsistencies in the attribution of qualities to cation and anion are understandable.

Beidler has reported electrophysiological evidence [6, 7, 8, 9] that the effectiveness of a salt in eliciting a response is

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determined primarily by the cation, although the anion plays some usually inhibitory role. Hydrated and dehydrated size of the cation, as well as the exact nature of the anion receptor site of the membrane molecule, may contribute to the effectiveness of the cation. Because the nature of the anionic receptor site can vary at different points along the membrane, the relative effectiveness of a homologous series of salts varies both within and across species [10].

The fact that the effectiveness of a given salt in eliciting an impulse in taste neurons of the rat (cat, etc.) is largely, if not completely, predictable by the size of the cation [9], does not allow prediction of the magnitude of any specific taste quality for man, although it may allow prediction of the total intensity of the salt. If, as is usually the case, the salt elicits more than one taste quality (e.g. bitter and salty for KCl) then the total intensity of the salt will reflect the combined magnitude of saltiness, the magnitude of any non-salty tastes of the compound, any accompanying water tastes (taste responses to water which depend on adaptation to a preceding stimulus [1, 3, 23]), and any effects of mixture suppression (a mixture interaction which produces a perceived intensity for a mixture which is less than the sum of the perceived intensities of its unmixed components [3,23]). Thus, in order to successfully attribute quality and/or intensity effects to the cation and/or anion, it is necessary to examine not only the overall intensity for both cationic and anionic series, but also the magnitudes of all qualities in evidence and suppressed.

Bartoshuk, Murphy, and Cleveland [5] established that the sweet taste of dilute NaCl is mediated by the same receptors that mediate the sweetness of other sweet stimuli, rather than being the result of a coding confusion. In that experiment, adaptation to sucrose not only cross-adapted [3,23] the sweetness of dilute NaCl, but also produced small increments in the sourness and saltiness of NaCl. It was suggested that the latter could have been a result of the release of mixture suppression. This notion was supported by the fact that both adaptation to sucrose and topical application of gymnema sylvestre produced similar increases in sourness and saltiness of NaCl. The present study examines the magnitude of sweetness, saltiness, sourness and bitterness at four concentrations of each of the following fifteen halide salts: LiCl, LiBr, LiI, NaCl, NaBr, NaI, KCl, KBr, KI, RbCl, RbBr, RbI, CsCl, CsBr and CsI.

In addition, similar techniques have been applied in an attempt to release mixture suppression of bitterness by saltiness, in order to examine the effects of both the anion and cation on the bitterness of 15 halide salts.

METHOD

Subjects

Six males and four females served. All but one had previous experience in psychophysical experiments.

Stimuli

LiCl, LiBr, LiI, NaCl, NaBr, NaI, KCl, KBr, KI, RbCl, RbBr, RbI, CsCl, CsBr, CsI, caffeine, sucrose, citric acid and distilled water served as stimuli. Each of the salts was prepared in the geometric concentration series: 0.108, 0.036, 0.012, and 0.004 M. The organic compounds were prepared in the following concentration series: 0.033, 0.0109, 0.0012 and 0.0004 M caffeine; 0.106, 0.035, 0.012 and 0.004 M sucrose; and 0.004, 0.0013, 0.0004 and 0.000133 M citric acid. There were, therefore, a total of 73 test solutions. All test compounds were reagent grade, prepared with distilled water and presented at room temperature (22°C).

Procedure

The experiment consisted of two conditions. In the first condition subjects rinsed their mouths with 25 ml of distilled water, then sipped 5 ml of the test stimulus. Subjects judged the perceived intensity of each of the 4 basic taste qualities (sweet, sour, bitter and salty) using the method of modulus-free-magnitude estimation [35]. Subjects judged each stimulus once within a single session, with one or two short rest intervals. All stimuli were presented in random order.

The second condition was distinguished from the first by a 0.5 M NaCl pre-rinse. The subject sipped 25 ml of 0.5 M NaCl, rinsed vigorously for 30 seconds and then expectorated before tasting each test stimulus. The "sip and spit" method was the method of choice in this experiment since the flow system method, usually employed for studies of adaptation and cross-adaptation, requires much larger quantities of stimuli. The concentration of the NaCl rinse was chosen on the basis of pilot work which showed it to be the lowest concentration that would completely adapt the saltiness of the most concentrated test stimuli under the whole mouth "sip and spit" condition. The second condition was conducted on a separate day and was identical in all other respects to the first. Since the experimental sessions required two days of testing, a small number of stimuli were presented under each condition for purposes of normalizing the magnitude estimation data.

Data Analysis

Geometric means (GM) of the magnitude estimates of total taste intensity were computed across all normalization stimuli for each subject and condition. In addition, a grand subject mean (GSM) was calculated across conditions for each subject. The raw magnitude estimates for each subject and condition were then multiplied by the ratio of that subject's GSM to his GM for each condition. This procedure placed all of a given subject's estimates on the same scale of magnitude. A similar normalizing procedure was used to place all subjects' ratings on the same scale of magnitude. Because of the large number of zeros in the raw data, a median, taken across all subjects for each quality, stimulus, and condition was used as the final measure of central tendency for these data.

RESULTS AND DISCUSSION

When presented after the water rinse, each of the salts tested showed quality shifts within the range of concentrations used (0.004–0.108 M). Figures 1–5 show these changes as reflected in the percentage of the total number of responses falling into the "sweet", "sour", "bitter", "salty", and "no taste" categories.

In general, for their respective anions, the lighter cations elicited a larger percentage of salty responses; whereas the heavier cations elicited a larger percentage of bitter responses, particularly at the higher concentrations.

With respect to the anion, the iodide salts generally evoked a larger percentage of bitter responses than did either the chloride or bromide salts.

Although the percent response measure gives an adequate view of the relative number of responses falling into each category, it provides no information concerning the mag-

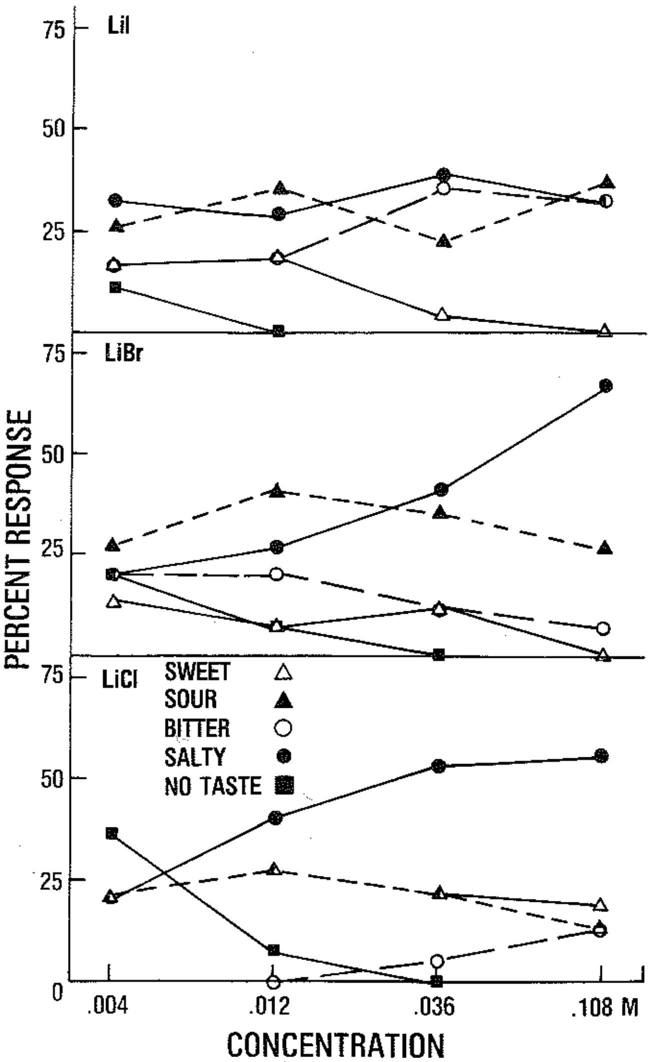

FIG. 1. Percentage of responses of the four gustatory qualities as a function of concentration of LiI (upper graph), LiBr (middle graph), and LiCl (lower graph).

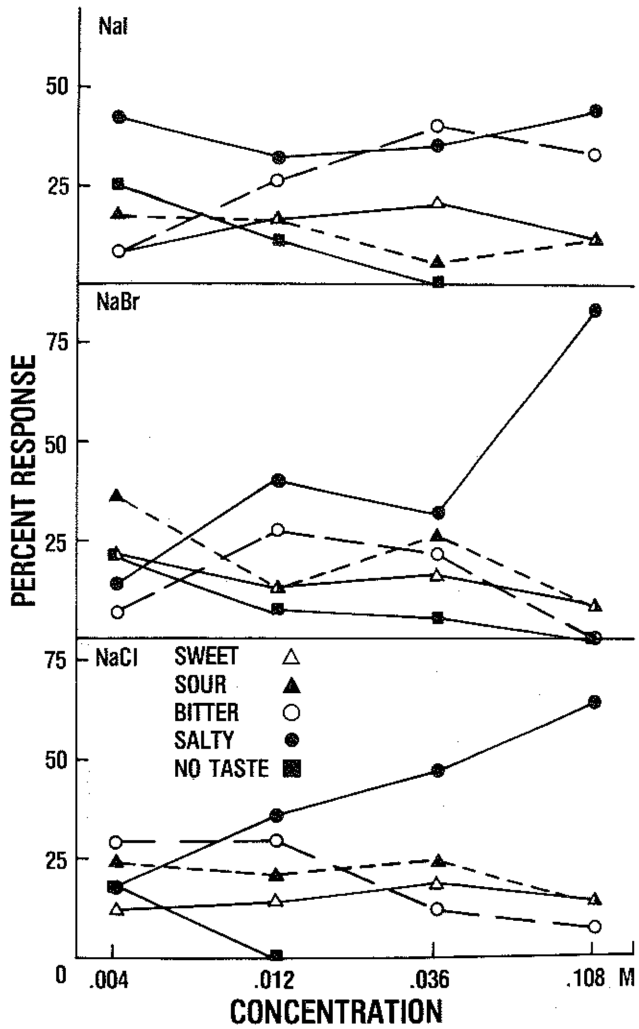

FIG. 2. Percentage of responses of the four gustatory qualities as a function of concentration of NaI (upper graph), NaBr (middle graph), and NaCl (lower graph).

nitude of these responses. Figures 6–10 show the median magnitude estimates of the sweet, sour, bitter and salty tastes for each of the salts. Because a median was used as the measure of central tendency, taste qualities that were ascribed to a particular stimulus by less than 50% of the subjects do not appear.

As shown in Fig. 6, both LiCl (lower graph) and LiBr (middle graph) are intensely salty at high concentrations. The moderate saltiness of LiI (upper graph) decreases from 0.036 to 0.108 M, whereas the small amounts of sour and bitter at 0.036 M increase and predominate over saltiness at 0.108 M.

Saltiness generally predominates over the other tastes for the sodium salts shown in Fig. 7, although bitterness is more intense than saltiness for 0.036 M NaI (upper graph) and slightly more intense for 0.004 M NaCl (lower graph).

As shown in Fig. 8, KCl (lower graph) and KBr (middle graph) show moderately intense saltiness at the highest concentration. Below 0.108 M, KCl is predominantly bitter, whereas KBr is approximately equally salty and bitter. KI (upper graph) is predominantly bitter at all concentrations, intensely so at 0.108 M.

Figure 9 shows the median magnitude estimates for the three rubidium salts: RbCl (lower graph), RbBr (middle graph) and RbI (upper graph).

RbCl is predominantly bitter from 0.004 M to 0.036 M and predominantly salty at the highest concentration. Some sweetness presents itself in the midrange. RbBr is predominantly bitter, but a large salty component is also present at 0.108 M. The bitter taste of RbI predominates at all concentrations, becoming very intense at 0.108 M.

Figure 10 shows the taste judgments for the three cesium salts: CsCl (lower graph), CsBr (middle graph) and CsI (upper graph).

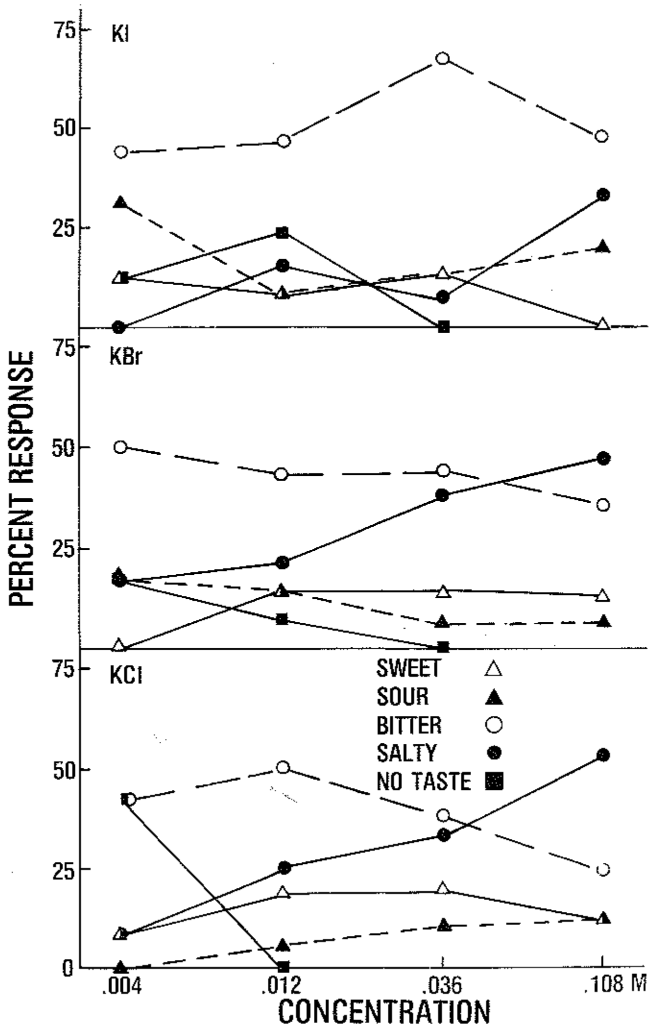

FIG. 3. Percentage of responses of the four gustatory qualities as a function of concentration of KI (upper graph), KBr (middle graph), and KCl (lower graph).

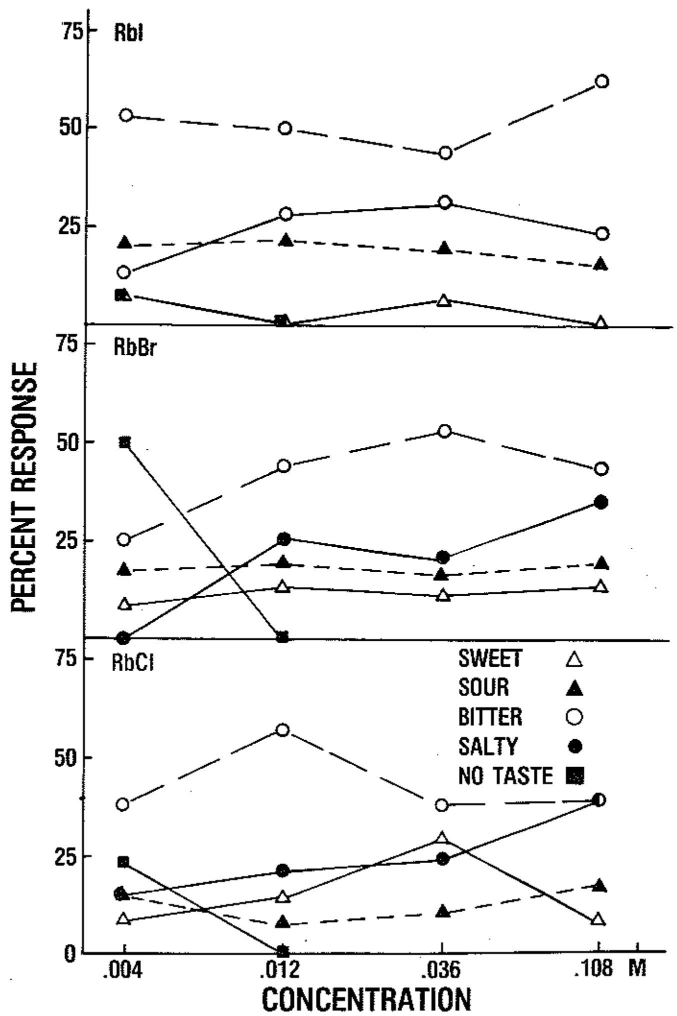

FIG. 4. Percentage of responses of the four gustatory qualities as a function of concentration of RbI (upper graph), RbBr (middle graph), and RbCl (lower graph).

CsCl is almost completely bitter at concentrations below 0.108 M. At 0.108 M saltiness slightly exceeds bitterness. CsBr is also predominantly bitter below 0.108 M, but at 0.108 M saltiness accounts for more than 60% of the total taste magnitude. CsI is consistently bitter at all concentrations.

At the highest concentration all salts were predominantly salty; except for LiI, KI, RbI, CsI and RbBr, each of which was predominantly bitter. NaI was the only iodide salt that was more salty than bitter at the highest concentration tested.

The data from both the water pre-rinse and salt pre-rinse conditions were also analyzed using multidimensional scaling. Multidimensional scaling has been shown to be useful in providing pictorial representation of the relationships among various chemosensory stimuli [27, 28, 31, 32]. Figure 11 shows the results in three dimensions which were achieved by MD-5SCAL for the data for the 15 salts presented after the water pre-rinse in this experiment. The analysis was performed on all data for all concentrations. The results are shown here plotted separately for each concentration. Within the 3-dimensional space generated by MD-5SCAL, the attributes salty and bitter form one dimension. A second dimension is defined by sweet and sour at one pole and salty and bitter at the other pole. On the third dimension the attributes are ordered bitter, sour, salty, sweet, with approximately the same distance between each attribute. Figure 11a, the results for the salts at 0.004 M, shows the tendency for the tastes of the salts at low concentrations to congregate nearer the bitter pole of the bitter-salty dimension, on the bitter-salty side of the second dimension and near the bitter pole of the third dimension. At the higher concentrations (Fig. 11b, c, d), the salts again fall near bitter-salty on the

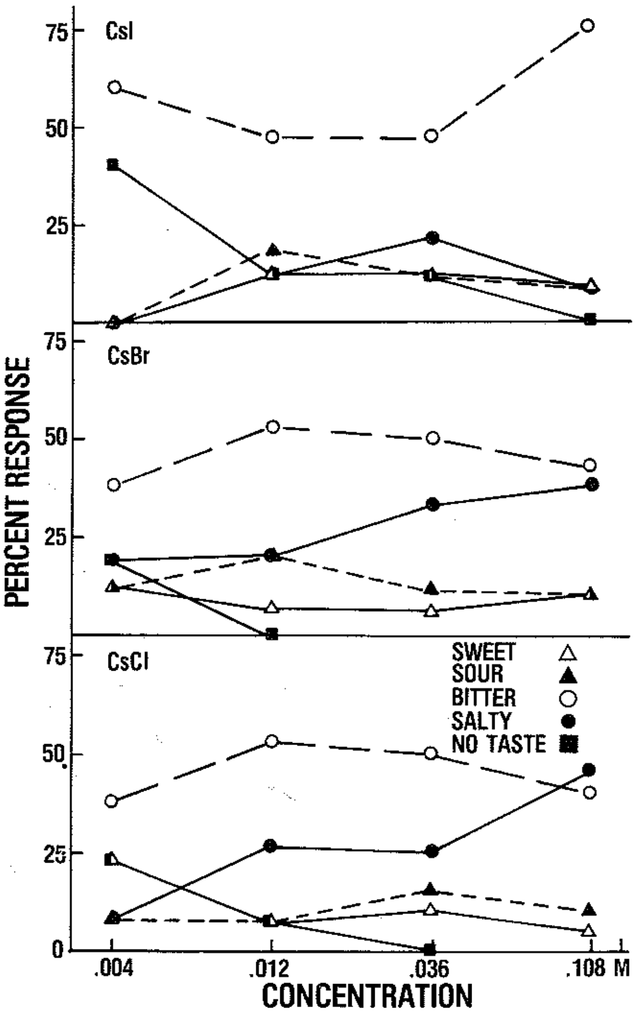

FIG. 5. Percentage of responses of the four gustatory qualities as a function of concentration of CsI (upper graph), CsBr (middle graph), and CsCl (lower graph).

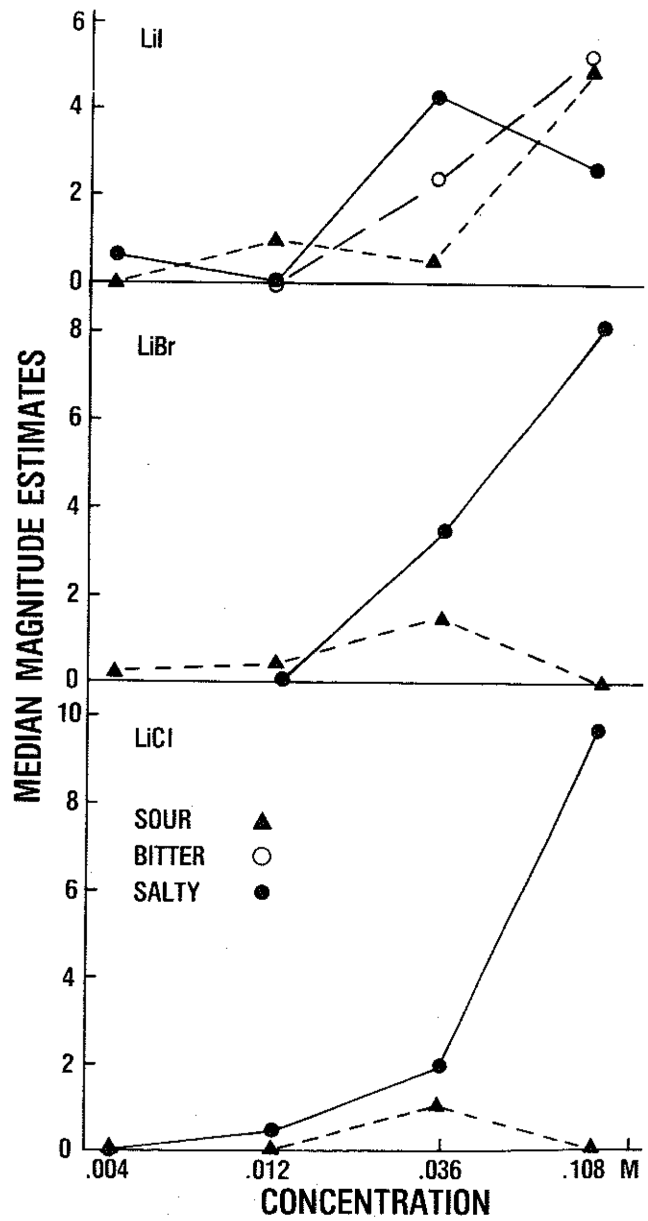

FIG. 6. Median magnitude estimates of the four gustatory qualities as a function of concentration of LiI (upper graph), LiBr (middle graph), and LiCl (lower graph).

second dimension and closer to the bitter pole on the third dimension. However, most salts have shifted toward the midpoint on the bitter-salty dimension (Dimension 1).

In order to examine the effects of cation and anion on the taste of the salts, unencumbered by the quality shifts at lower concentrations, the taste quality data for the 0.108 M solutions were statistically analzyed for their relationship to cationic, anionic and molecular weight of the salt. While there was no systematic effect of the molecular weight of the salt on the magnitude of any taste quality, or on total perceived intensity, examination of the individual effects of cationic and anionic weights revealed several significant effects on perceived saltiness and bitterness. Perceived bitterness increased significantly as the weight of the cation increased (see lower portion of Fig. 12). Although the relationship is not ideal, viz. the values for LiI and CsBr; the effect is statistically significant at the 0.001 level as measured by the Friedman two-way analysis of variance (ANOVA): $\chi_r^2=228.21$.

The upper portion of Fig. 13 shows the effect of anionic weight on the saltiness of the salts at 0.108 M. With one exception (NaBr) the heavier anions produced less saltiness for each of the cations tested. A Friedman two-way ANOVA performed on the saltiness judgments for the chloride, bromide and iodide groups showed the effect of anionic weight to be statistically significant at the 0.001 level: $\chi_r^2=37.0$. Anionic weight also had significant effects on the bitterness of these salts, as seen in the lower portion of Fig.

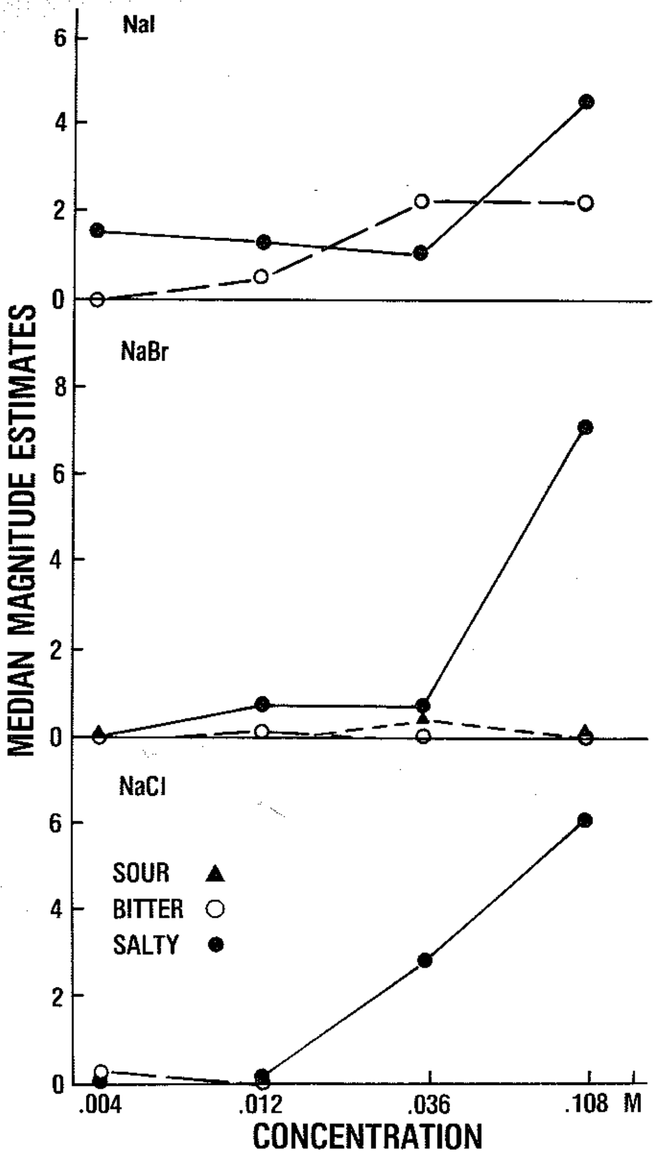

FIG. 7. Median magnitude estimates of the four gustatory qualities as a function of concentration of NaI (upper graph), NaBr (middle graph), and NaCl (lower graph).

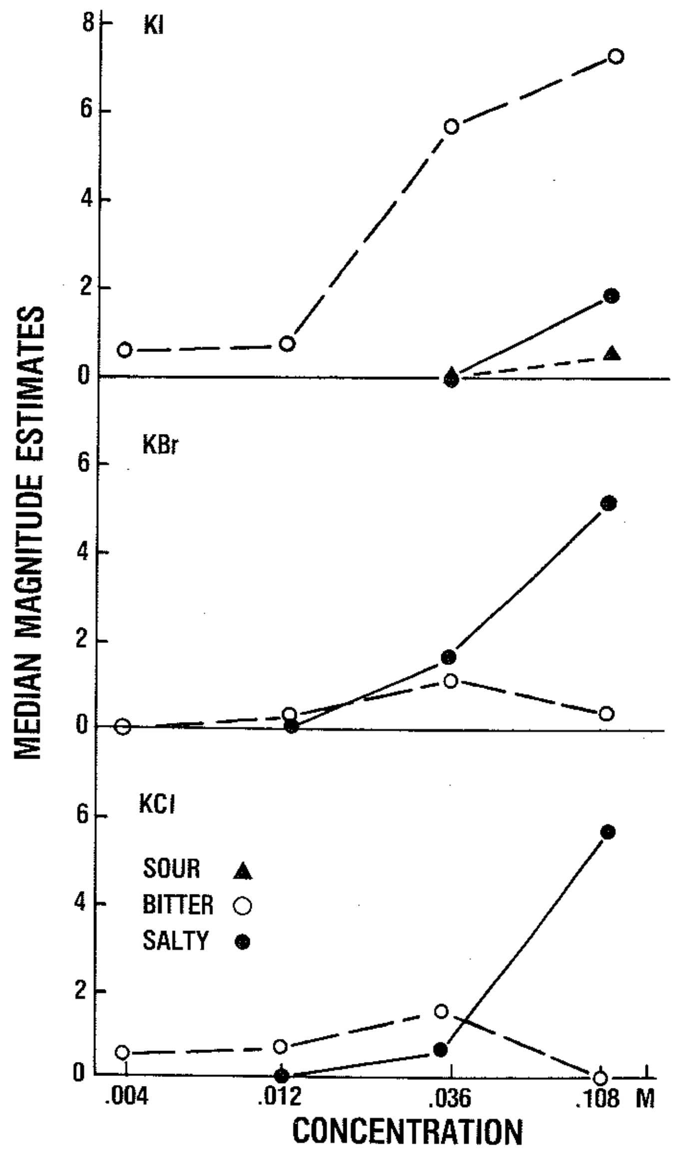

FIG. 8. Median magnitude estimates of the four gustatory qualities as a function of concentration of KI (upper graph), KBr (middle graph), and KCl (lower graph).

13. A Friedman ANOVA performed on the bitterness judgments for the chloride, bromide and iodide salts was again significant at the 0.001 level: $\chi_r^2=35.62$.

No subject in the present experiment attributed any saltiness to NaCl at any concentration following the 0.5 M NaCl pre-rinse. Hence, complete adaptation has been demonstrated under the conditions of this experiment.

Earlier studies of cross-adaptation have given rise to the generalization that salts with common cations usually produce the greatest cross-adaptation. This was only partly true in the present experiment. The saltiness of each salt was virtually eliminated by adaptation to the 0.5 M NaCl. However, since the bitterness of some salts increased following cross-adaptation (see Fig. 14), overall intensity was higher after NaCl adaptation for some salts but not for others. Smith and McBurney [34] obtained similar results with the monovalent halides NaCl, NaBr, KCl and KBr. In the present study, NaCl showed complete self-adaptation, and NaBr showed almost complete cross-adaptation. These results seem to support the above generalization regarding common cations. However, both LiCl and LiBr also showed almost complete cross-adaptation and NaI showed a sevenfold increase in bitterness after the salt rinse. Perceived bitterness of NaI was lower than any other iodide salt, but greater than any of the chloride or bromide salts of any of the tested cations. In fact, all of the iodide salts showed large increases in bitterness following cross-adaptation.

A Friedman ANOVA performed on the judgments for

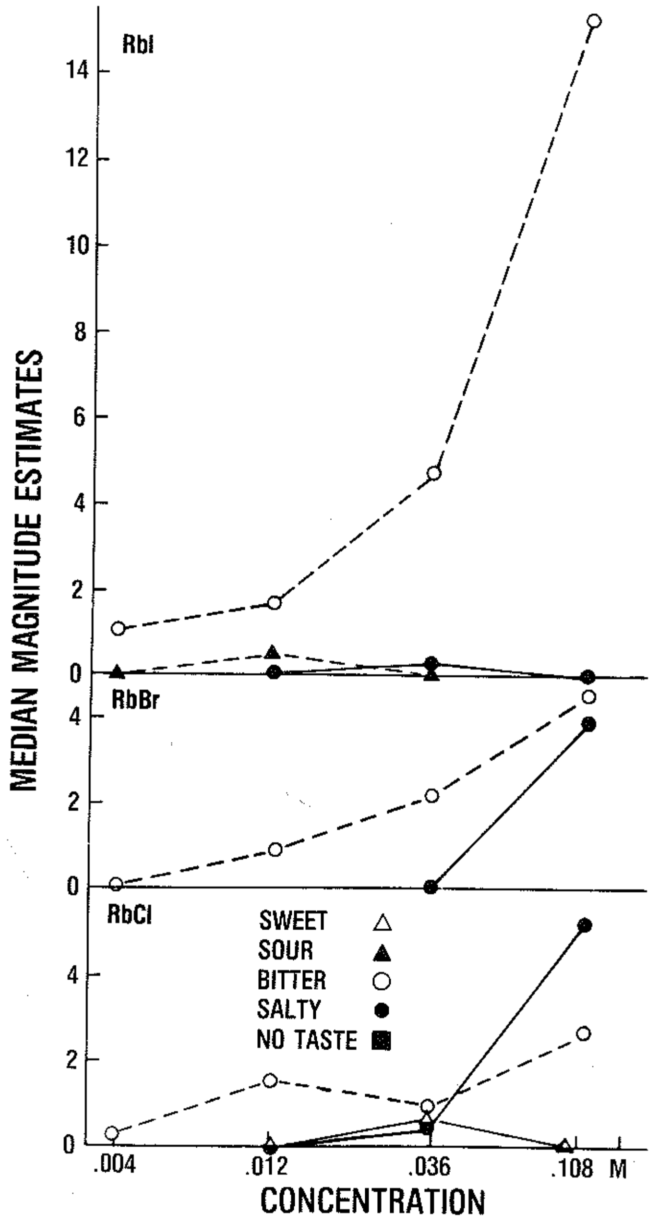

FIG. 9. Median magnitude estimates of the four gustatory qualities as a function of concentration of RbI (upper graph), RbBr (middle graph), and RbCl (lower graph).

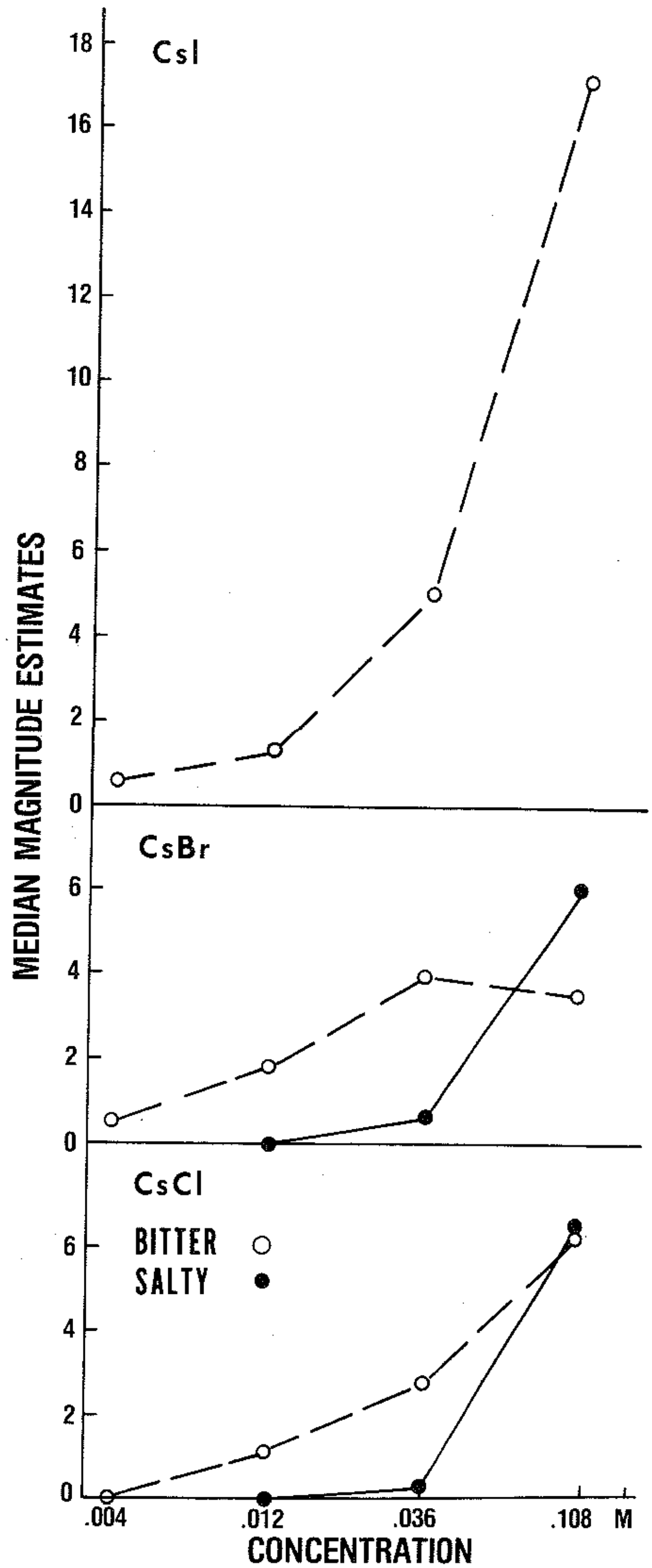

FIG. 10. Median magnitude estimates of the four gustatory qualities as a function of concentration of CsI (upper graph), CsBr (middle graph), and CsCl (lower graph).

bitterness after water and bitterness after NaCl for each of the iodide salts showed the effect to be statistically significant at the 0.01 level ($\chi_r^2=9.68$). A similar ANOVA performed on the judgments for the chloride and bromide salts was non-significant. Thus, the effect of anionic weight on the intensity of bitterness is magnified following cross-adaptation.

Both cation and anion, then, appear to influence the magnitude of taste following cross-adaptation. This is particularly evident in cases of salts whose taste profiles are distinctly different from that of the adapting salt.

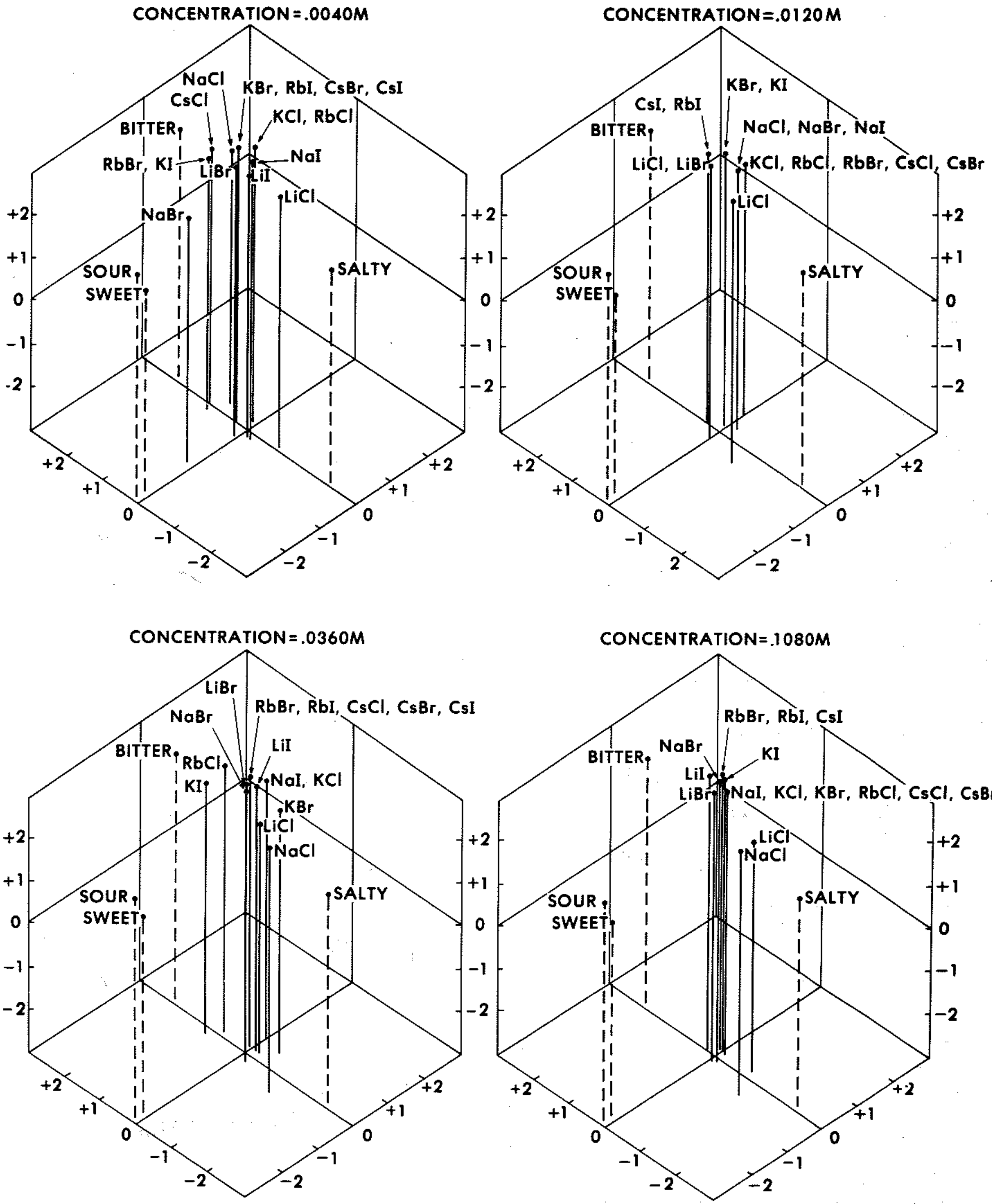

FIG. 11. Three dimensional solution achieved by MD-5SCAL for the data from the fifteen salts at each of the four concentrations: (a) 0.004 M, (b) 0.012 M, (c) 0.036 M, (d) 0.108 M.

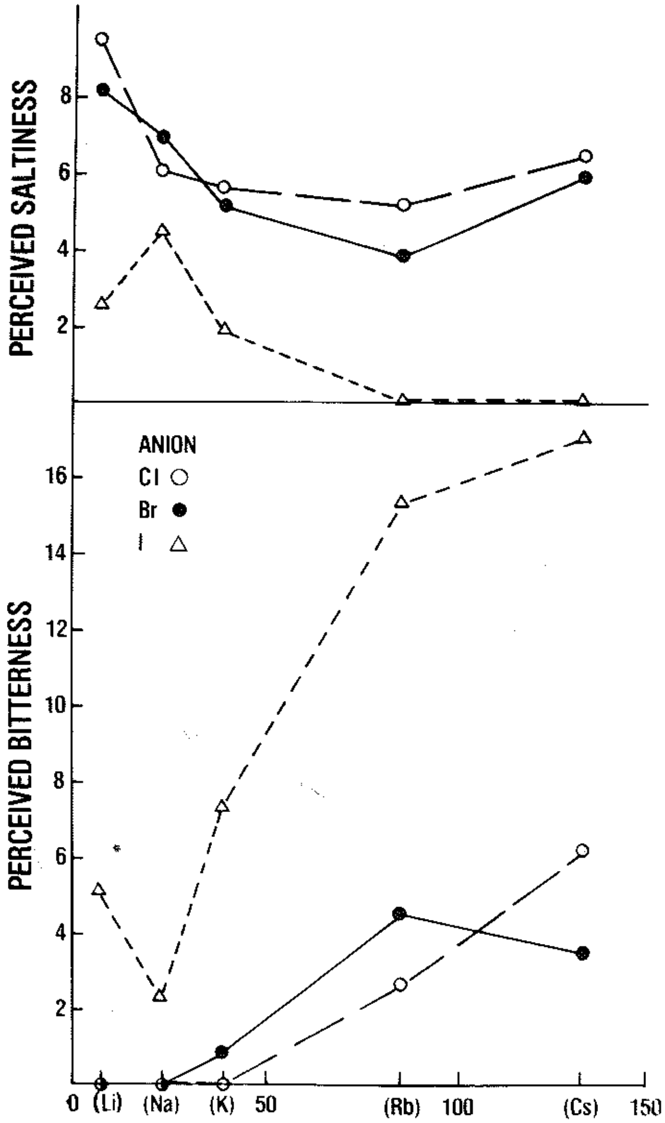

FIG. 12. Perceived saltiness (upper graph) and perceived bitterness (lower graph) of each of the fifteen halides at a concentration of 0.108 M, as a function of cationic atomic weight. Stimuli were preceded by a water rinse.

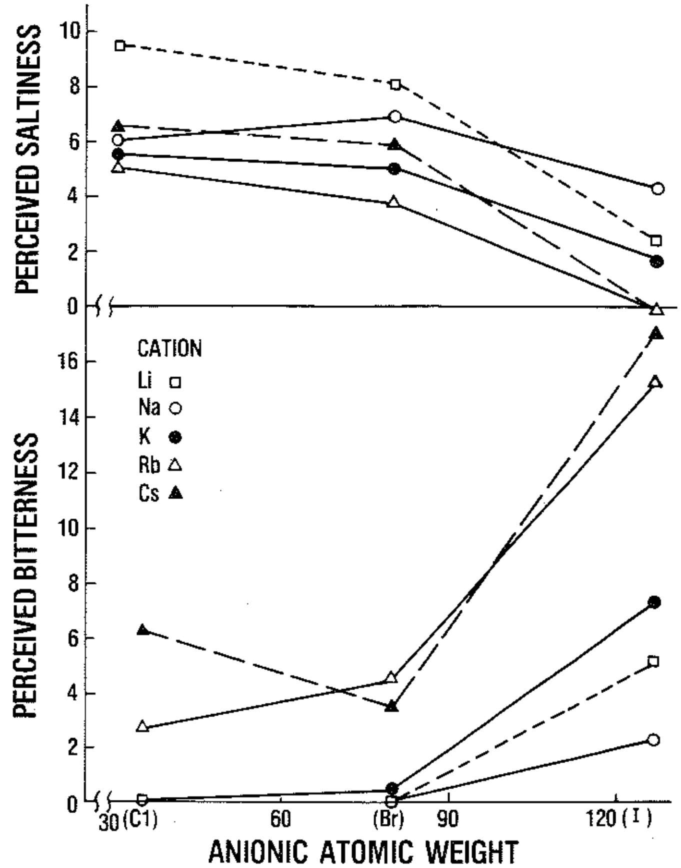

FIG. 13. Perceived saltiness (upper graph) and perceived bitterness (lower graph) of each of the fifteen halide salts at a concentration of 0.108 M, as a function of anionic atomic weight. Stimuli were preceded by a water rinse.

Since NaCl produces sour-bitter, but predominantly bitter, water taste [1–4, 23], could the increase in bitterness following adaptation be the result of the addition of water tastes following NaCl adaptation? Bartoshuk [1] pointed out that if an observed effect is due to water taste, it should increase as concentration decreases; whereas if the effect is due to the compound being tested, it should increase as concentration increases. Applying this principle to the bitterness after cross-adaptation of the salts in this experiment it is clear that the effect cannot simply be attributed to the water taste. Figure 15 illustrates that for each of the iodide salts, bitterness increases with each increase in concentration.

Even those salts which do not show substantial increases in bitterness after adaptation to NaCl, but which do show some bitterness after NaCl, (essentially, every non-iodide salt with molecular weight greater than 120) exhibit the same pattern of bitterness increasing with concentration (see again Fig. 15).

Each of the iodide salts increased in bitterness following adaptation to NaCl. The other salts shown in Fig. 15 showed bitterness levels after adaptation which were at, or slightly below, those displayed after the water rinse. These latter salts may provide a key to the degree of complexity of the mixture interactions involved in the tastes of monovalent halide salts. A small decrease in bitterness following adaptation could be due to some degree of across quality adaptation of the salt by NaCl. McBurney and Bartoshuk [24] found some degree of cross-adaptation between the majority of 18 pairs of compounds of different qualities, an effect which they attributed to an interaction between the water taste and the solute taste of a compound following adaptation. The sourness of a sour-bitter water taste could conceivably produce a small decrement in the already mild bitterness of a salt such as RbCl.

Following the salt rinse there was a statistically significant increase in the sweetness of several salts: NaCl, KCl,

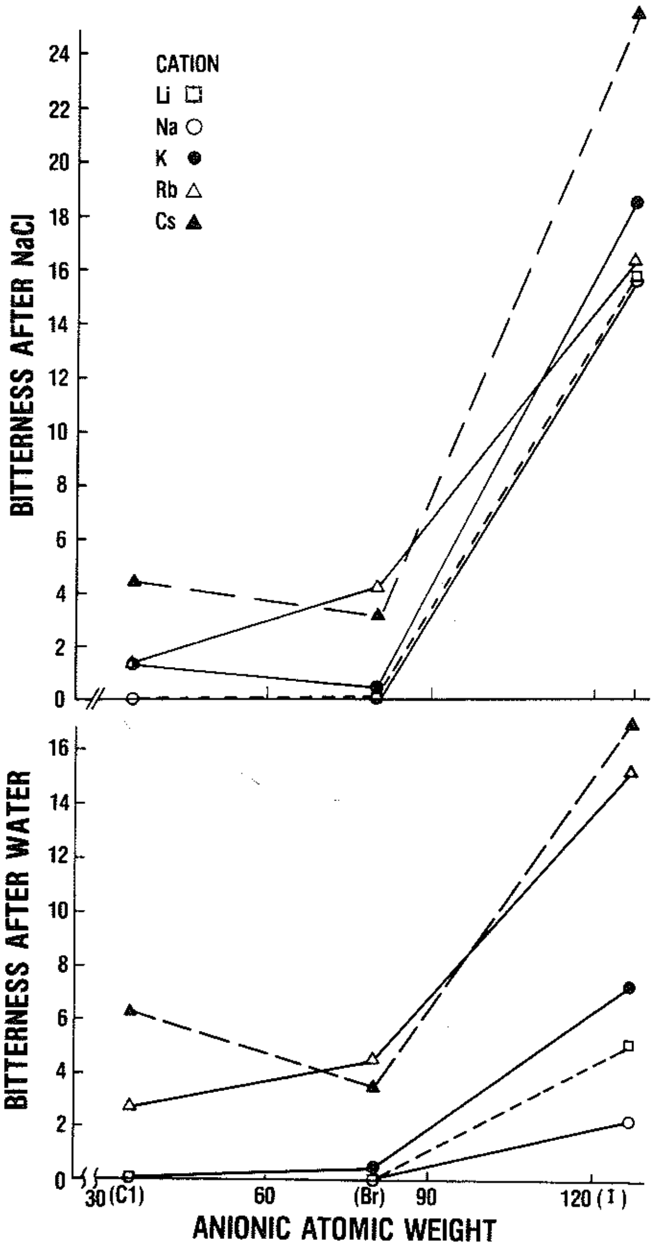

FIG. 14. Perceived bitterness of each of the fifteen halides at a concentration of 0.108 M, as a function of anionic atomic weight. The lower graph shows responses following a water rinse; the upper graph shows responses following a NaCl rinse.

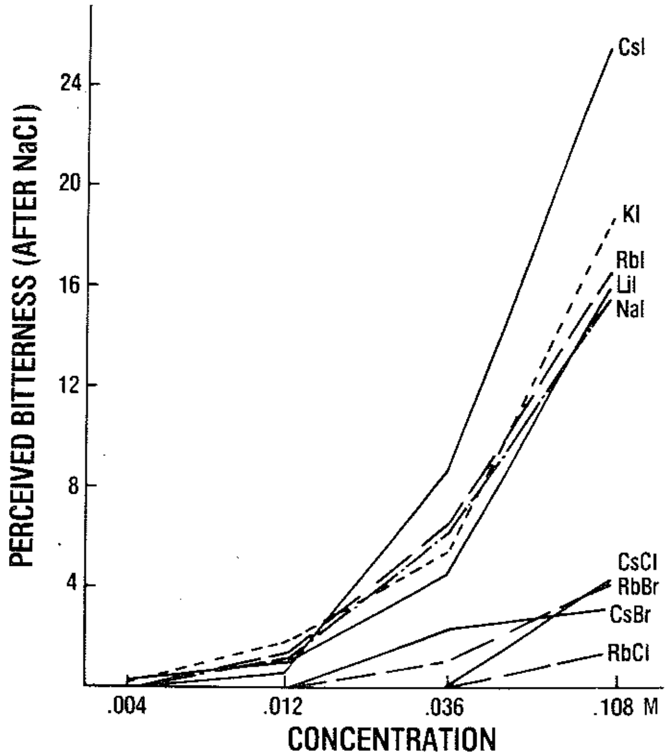

FIG. 15. Perceived bitterness of each of the fifteen halides as a function of concentration, plotted semi-logarithmically. Simuli were preceded by a NaCl rinse.

RbCl, CsCl, KBr and RbBr; relative to the levels shown after the water rinse (Friedman two way ANOVA, $p<0.001$, $\chi_r^2=35.47$). Sweetness is not a typical water taste response to NaCl [1, 2, 4, 26]. Furthermore, examination of the responses of individual subjects revealed no significant increase in the sweetness of any of these six salts with decreasing concentration. All six Friedman ANOVA's comparing magnitude of sweetness judgments across concentration were non-significant. Hence, the small increases in sweetness after NaCl seen for NaCl, KCl, RbCl, CsCl, KBr and RbBr cannot be attributed to a water taste. The more likely explanation is the release of mixture suppression produced by saltiness. As a result, sweetness is available to interact in complex ways with the bitterness and sourness of the solute-solvent combination. Adapting out any sour and sweet tastes present after adaptation to NaCl could conceivably alter the bitterness judgments after NaCl shown in Fig. 14, and modify the apparent effect of anionic atomic weight on perceived bitterness.

Both cation and anion contribute to the tastes of the halide salts. In general, ions of higher atomic weight result in salts that taste increasingly bitter and decreasingly salty. These observations should not immediately be taken as an indication that the salts' ability to impart bitterness is simply a reflection of its ability to impart saltiness. Bitterness and saltiness arise from two different receptor systems although it is possible that the intrinsic properties of the salt in question can excite both receptor systems to varying degrees and even that a property that may inhibit one system may excite the other.

DeSimone and Price [13] have hypothesized that electrostatic interactions between the essentially negative receptor plasma membrane of the taste cell and the positive cations of salts are responsible for an ultimate change in receptor charge density which, in turn, initiates intracellular processes that lead to release of synaptic vesicular contents in the taste cell [11]. In light of the present data, we may assume that the positive ions all have some ability to electrostatically interact with the salt receptor membrane and thus all have, albeit to varying degrees, some ability to generate the response "salty." It is apparent when examining the chloride series for the cations, Li, Na, K, Rb, Cs that, at any given concentration, the heavier cations excite salty receptors to a degree less than the lighter ones, Li and Na. At the same time, however, it is obvious that heavier cations will yield an increasingly bitter response in subjects, provided the same anion is compared. Both of these observations may be mechanistically related to the known ability of the positive ions in the lyotropic series to differentially interact with the lipid phase of plasma membranes [11, 16, 29]. For example, one of us has observed (Brand and Bayley, unpubished observations) that at equimolar concentrations, the heavier the cation, the less is its ability to alter the charge density of a liposome suspension as measured by a fluorescent dye. We are thus left with the speculation that both saltiness and bitterness may be due to properties of the cation, with a tendency for saltiness to be associated with the cations of lower atomic weight and bitterness to be associated with cations of higher atomic weight.

The present study also contains a very obvious anion effect, where increasing anionic atomic weight leads to less saltiness and more bitterness. While this trend is not strong between Cl and Br, it is very strong between Br and I. DeSimone and Price [13] speculate that the well known suppressive effect of anions on saltiness is due to ion pair formation. Thus, for any given cation, any series which yields increasing ion pair formation should also yield decreasing saltiness. This hypothesis can be tested directly using the current experimental results, if we have a method of estimating potential ion pair formation. To do this, one can calculate the ionic character of each salt based on an empirical formula of Hannay and Smyth [17]. This formula assumes knowledge of individual elemental electronegativities. Using those tabulated by Little and Jones [21], one can make approximations of percent ionic character. Our use of the concept of percent ionic character is not meant to suggest that we envision a significant concentration of uncharged (essentially molecular) ion pairs in aqueous solution. The high dielectric constant of water would preclude this possibility except at very high salt concentrations. Rather, we employ this concept and the empirical formula for percent ionic character only as an index of possible ion pair formation within the compact region of the plasma membrane surface. It is in this region that the solvent dielectric constant should be lower than that of the bulk medium [13] thus promoting possible ion pairs. When percent ionic character is calculated, one finds that regardless of the cation chosen, the series Cl, Br, I leads to decreasing percent ionic character with a particularly pronounced separation between Br and I. For example, the percent ionic characters of the series KCl, KBr, KI are 43.6, 41.0 and 26.7 respectively; those of CsCl, CsBr and CsI are 45.1, 42.4 and 28.0, respectively. Loss of saltiness could then be, as DeSimone and Price suggest, due to ion pair formation. A particularly striking example of not only this anion suppressive effect but also of the general loss of saltiness with increasing cationic atomic weight can be seen with the salt CsI, which yields almost no saltiness response at all (Figs. 5 and 10).

Bitterness of the heavier cations may also be augmented by ion pair formation such that, with the heavier cations causing increasing bitterness, the heavier anions augment this bitterness through ion pair formation. Alternatively, the marked increase in bitterness observed on the transition from Br salts to I salts could lead one to speculate that iodide itself contributes significantly to bitterness. Calculations of the percent ionic character of the iodide salts show that CsI would have the most ionic character, NaI the least. This, in turn, would lead one to predict that if I^- is a bitter stimulus, then bitterness of the iodides should increase in the series

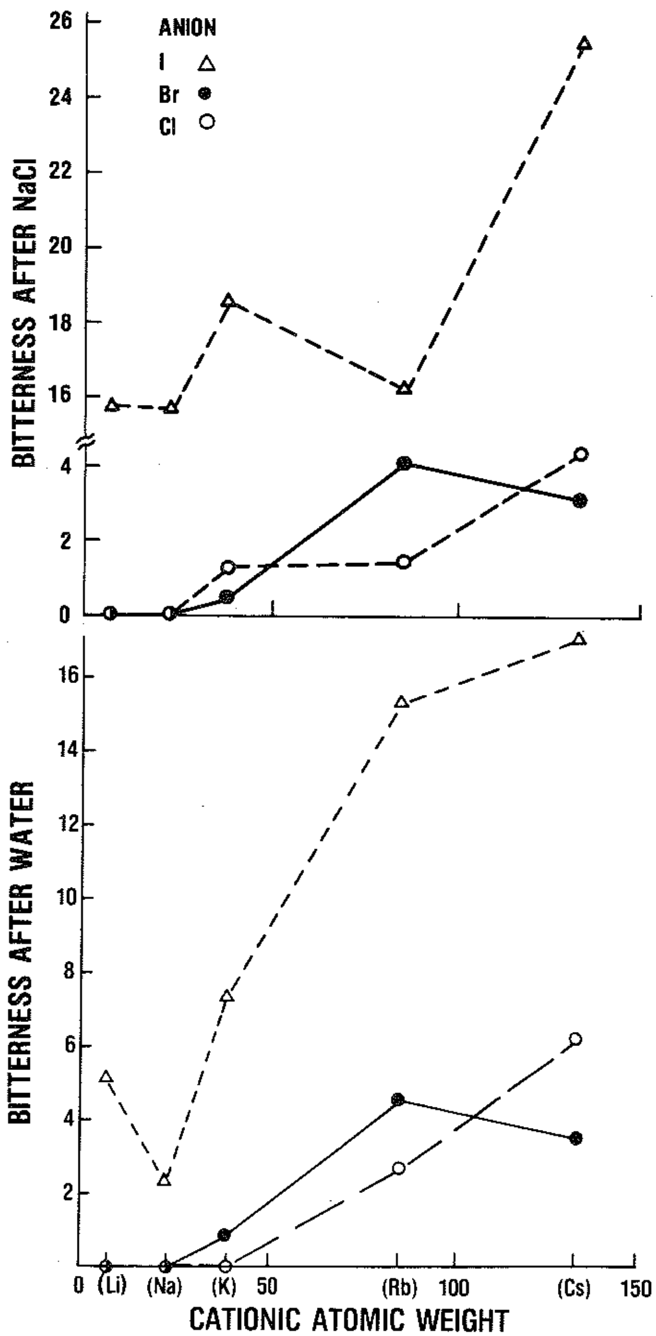

FIG. 16. Perceived bitterness of each of the fifteen halides at a concentration of 0.108 M, as a function of cationic atomic weight. The lower graph shows responses following a water rinse; the upper graph shows responses following a NaCl rinse.

Na<Li<K<Rb<Cs. This series is, in fact, observed (Fig. 14). Of course, what is disturbing about this hypothesis is the necessity of assuming a close approach of a negative anion toward a sheet of negative charge, that is, the plasma membrane. One would predict, then, that if this mechanism is plausible, partial neutralization of the negative plasma membrane should augment the bitterness of the iodide salts. This study has shown just such an effect when the tongue is adapted to 0.5 M NaCl, where, presumably, the positive Na^+ acts to decrease the effective negative charge of the plasma membrane. Since the bromide and chloride ions will hold a negative charge more tightly than iodide ions, they should not be able to approach the plasma membrane as readily as iodide.

Even if iodide were a bitter stimulus, we have the perplexing problem of having just assumed that both heavy positive cations and heavy negative anions can excite the bitter receptor cell. Since no single receptor moiety could accomodate this charge dichotomy, it must be that either there is more than one type of receptor for bitterness, or the anion is not the stimulus. Whatever properties of the ions that may be responsible for these effects—atomic or hydrated radii, electronegativities, ion pair formation, etc.—it is clear from these data that there are very marked effects of both cation and anion on psychophysical response. These results can lead to both psychophysical and biochemical experiments that should seek to understand the receptor mechanisms involved in salty and bitter reception.

CONCLUSIONS

The results of the present study support the existence of low-concentration non-salty tastes for all fifteen halide salts studied. Furthermore, these non-salty tastes were involved in complex mixture interactions with salty as well as non-salty tastes. Failure to take these complex mixture interactions into account may confuse results of studies designed to show anionic and cationic effects on the tastes of the halide salts.

Previous investigators have demonstrated non-salty or side tastes at low-concentration for many other salts, including: $LiSO_4$, KSO_4 [12,13]; NH_4Cl, NH_4Br, NH_4I [19,30]; $MgCl_2$, $CaCl_2$, $BaCl_2$, $KClO_3$ $KClO_4$, KF, Na acetate, Li acetate and Ca acetate [20,30]. In these cases, and undoubtedly others, the presence of complex mixture interactions should be considered before drawing conclusions concerning the relative effects of cation and anion in determining the tastes of salts.

The present study also both confirms the existence of mixture suppresion by the various taste qualities elicited by a given halide salt and demonstrates release of mixture suppression through cross-adaptation.

Both cation and anion contribute to the tastes of the halide salts. Both heavier cations and heavier anions generally result in more bitter tasting salts (Figs. 12 and 13). Weight of the cation does not have a consistent effect on the saltiness of the salt, but lighter anions produce saltier salts (Figs. 12 and 13). Removing the saltiness of the halides through cross-adaptation to NaCl increases the bitterness of the salts of the heavier anions, but has minimal effect on bitterness as a function of cationic weight (Figs. 15 and 16).

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